

Robustness Against Extinction by Stochastic Sex Determination in Small Populations

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Abstract

Sexually reproducing populations with small number of individuals may go extinct by stochastic fluctuations in sex determination, causing all their members to become male or female in a generation. In this work we calculate the time to extinction of isolated populations with fixed number N of individuals that are updated according to the Moran birth and death process. At each time step, one individual is randomly selected and replaced by its offspring resulting from mating with another individual of opposite sex; the offspring can be male or female with equal probability. A set of N time steps is called a generation, the average time it takes for the entire population to be replaced. The number k of females fluctuates in time, similarly to a random walk, and extinction, which is the only asymptotic possibility, occurs when $k = 0$ or $k = N$. We show that it takes only one generation for an arbitrary initial distribution of males and females to approach the binomial distribution. This distribution, however, is unstable and the population eventually goes extinct in $2^N/N$ generations. We also discuss the robustness of these results against bias in the determination of the sex of the offspring, a characteristic promoted by infection by the bacteria *Wolbachia* in some arthropod species or by temperature in reptiles.

I. INTRODUCTION

Most species in our planet have small numbers of individuals [1]. Even the human population, now with more than seven billion people, has gone through periods of very low abundances not too long ago [2]. In fact, typical abundance distributions of several groups of species has been shown that follow a universal lognormal curve with an excess of rare species [1, 3].

Small communities are prone to extinction for a large number of reasons, such as inability to protect themselves or difficulty in finding mates [4], accumulation of deleterious mutations [5] and shear stochastic fluctuations in the environment [6–8] or in the number of males and females in the group [9]. If male and female offspring are equally likely to occur, the ratio between males and females fluctuates over generations [10] and it might occur that they all become male or female, driving the population to extinction. This works against the persistence of small communities and it is somewhat puzzling how so many such populations do exist. In some species, the females developed ways to control the sex ratio of their progeny, producing more females in a male rich environment and vice-versa. This mechanism, termed local mate competition [11, 12], may have evolved to avoid extinction by fluctuations in sex determination.

In this work we consider the changes in the sex ratio of a population with fixed number of individuals in which a single member is randomly selected to reproduce at each time step, being replaced by a male or a female offspring with equal probability. The model is a great simplification of the dynamics of real populations, but it captures the random character of the process and sheds light on why low abundance species are actually much more robust than one could naively expect. In particular, we do not take into account the fact that females usually have many offspring and, even if the population size is held fixed, there is competition among the offspring and it is the best fit individual who survives. In a population consisting mostly of males, it is expected that a female offspring will fare better than a male, contributing to balance the sex ratio. We shall not take competition, natural selection, spatial structures [13] or aging into account [9], restricting our work to *neutral* evolution, which has been shown to describe the observed universal patterns of abundance and diversity, both for hermaphroditic and sexual populations [14–16].

II. THE DYNAMICAL SYSTEM

We consider a population with N individuals divided into k females and $N - k$ males. We call $P_t(k)$ be the probability of finding k females at time t . The population is updated at discrete time steps similarly to the birth and death process proposed by Moran in population genetics [17]: at each time step a random individual is selected to reproduce with an available member of the opposite sex; after reproduction the selected individual dies and is replaced by the offspring, which can be male or female with equal probability. The states $P(0)$ and $P(N)$ are absorbing states corresponding to *all males* and *all females* respectively and mark the extinction of the population, since reproduction becomes impossible when all members have the same sex. In a state with k females, the probability of having $k - 1$ females in a single time step is $\Omega_{k,k-1} = k/2N$, since one of the females has to be selected (probability k/N) and be replaced by a male offspring (probability $1/2$). Similarly, the probability of changing to a state with $k + 1$ females is $\Omega_{k,k+1} = (N - k)/2N$ and that of remaining with k females is $\Omega_{k,k} = 1/2$. The dynamics is similar to a random walk in the space of integers $0 \leq k \leq N$ biased towards $k = N/2$: the closer k is to 0 the smaller the probability of $k \rightarrow k - 1$; the closer k is to N the smaller the probability of $k \rightarrow k + 1$. This tends to stabilize the population, leading to small extinction probabilities. We define a generation by N time steps, which is the average time it takes for the entire population to be replaced.

The dynamics of $P_t(k)$ is governed by the following equations:

$$\begin{aligned}
P_{t+1}(0) &= P_t(0) + \frac{1}{2N}P_t(1) \\
P_{t+1}(1) &= \frac{N}{2N}P_t(1) + \frac{2}{2N}P_t(2) \\
P_{t+1}(k) &= \frac{N - k + 1}{2N}P_t(k - 1) + \frac{N}{2N}P_t(k) + \frac{k + 1}{2N}P_t(k + 1), \quad k = 2, 3, \dots, N - 2 \\
P_{t+1}(N - 1) &= \frac{2}{2N}P_t(N - 2) + \frac{N}{2N}P_t(N - 1) \\
P_{t+1}(N) &= \frac{1}{2N}P_t(N - 1) + P_t(N).
\end{aligned} \tag{1}$$

The probabilities $P_t(k)$ define a vector of $N + 1$ components P_t , in terms of which the

master equation above becomes

$$P_{t+1} = UP_t. \quad (2)$$

The evolution matrix U and the transition matrix $\Omega = U^T$ are tridiagonal. This is a linear system that can be completely solved in terms of the eigenvalues and eigenvectors of U . However, because U is not symmetric, both right \vec{a}_r and left \vec{b}_r eigenvectors are needed. Moreover, since $\sum_i U_{ij} = \sum_i \Omega_{ji} = 1$, U is a *stochastic matrix*, having real eigenvalues satisfying $\lambda_i \leq 1$ and

$$\sum_{r=0}^N \vec{a}_r \cdot \vec{b}_r^T = \mathbf{1} \quad (3)$$

where the superscript T stands for transposition, the lower dot represents the diadic product and the normalization is set by $\vec{b}_i^T \cdot \vec{a}_j = \delta_{ij}$. Using this property, the transition probability between an initial state with k_0 females and a state with k females after the time t can be written as

$$P(k, t; k_0, 0) = \sum_{r=0}^N b_{rk_0} a_{rk} \lambda_r^t \quad (4)$$

where a_{ri} is the i -th component of the r -th right eigenvector and similarly for b_{rj} . Equation (1) is an example of a Markov chain, a discrete dynamical system where the transition probability between any two states depends only on the two states involved and not on the past history of the system. Markov chains are ubiquitous in genetics [17–27], but not so common in population dynamics.

The dynamical system described by Eq.(1) is related to the one dimensional motion of a Brownian particle subjected to an external force $F(x)$, studied by Smoluchowski and Kac [28]. In this case the probability $P(x, t)$ of finding the particle at position x at time t satisfies the diffusion equation

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial x^2} - \frac{1}{f} \frac{\partial}{\partial x} (PF) \quad (5)$$

where D and f are the diffusion and friction coefficients. In the limit of large N we may set $\epsilon = 1/N$, $x_k = k\epsilon$ and the time step to δ and transform equation (1) into a similar equation,

$$\frac{\partial P}{\partial t} = \frac{\epsilon^2}{4\delta} \frac{\partial^2 P}{\partial x^2} + \frac{\epsilon}{\delta} \frac{\partial}{\partial x} [(x - 1/2)P]. \quad (6)$$

The ‘diffusion coefficient’ is $\epsilon^2/4\delta$ and the ‘force’ is harmonic, $F(x) = -(x - 1/2)$, tending to restore the population towards $x = 1/2$ (or $k = N/2$). The main difference between Eqs.(1) and (6) is that in the former the end points of the diffusion interval are absorbing states, lending the stationary solution of this equation unstable for any finite N .

Since each of the N individuals can be either male or female and only one individual is replaced at each step, the dynamics described by Eqs.(1) can also be mapped into a random walk to nearest neighbors in a hypercube in N dimensions [29]. This problem, it turn, is also related to the Ehrenfest model, where N numbered balls are placed into two boxes and at each time step one ball is chosen at random and moved to the other box [28]. Starting with all balls in one of the boxes and letting the system evolve corresponds to the classic model of a gas confined in one of two chambers and removing the wall separating the chambers. The state corresponding to all individuals of the same sex maps into two opposing corners of the hypercube and to all balls in the same box.

In this paper tackle the problem of sex ratio fluctuations in population dynamics and make contact with these classic statistical models. Some of the known analytical results available in the literature cited above will be connected to the present calculations below.

III. ABSORBING AND TRANSIENT STATES

The eigenvectors corresponding to $\lambda = 1$ completely determine the asymptotic behavior of the system, since the contributions of all the others die out at long times.

The evolution matrix U is given explicitly by

$$U = \left(\begin{array}{c|cccccccc|c} 1 & \frac{1}{2N} & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 \\ \hline 0 & \frac{1}{2} & \frac{2}{2N} & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{N-1}{2N} & \frac{1}{2} & \frac{3}{2N} & 0 & \dots & 0 & 0 & 0 & 0 & 0 \\ \vdots & \vdots & \dots & \dots & \vdots & \dots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & \dots & \dots & \dots & 0 & \frac{3}{2N} & \frac{1}{2} & \frac{N-1}{2N} & 0 \\ 0 & 0 & \dots & \dots & \dots & \dots & 0 & 0 & \frac{2}{2N} & \frac{1}{2} & 0 \\ \hline 0 & 0 & \dots & \dots & \dots & \dots & 0 & 0 & 0 & \frac{1}{2N} & 1 \end{array} \right). \quad (7)$$

There are two eigenvalues 1, with eigenvectors

$$\vec{a}_0 = \begin{pmatrix} 1/2 \\ 0 \\ 0 \\ \vdots \\ 0 \\ 1/2 \end{pmatrix} \quad \text{and} \quad \vec{a}_N = \begin{pmatrix} 1/2 \\ 0 \\ 0 \\ \vdots \\ 0 \\ -1/2 \end{pmatrix} \quad (8)$$

such that $\vec{a}_0 + \vec{a}_N$ corresponds to $P(0)$ and $\vec{a}_0 - \vec{a}_N$ to $P(N)$, both leading to extinction. The corresponding left eigenvectors are

$$\vec{b}_0 = \begin{pmatrix} 1 \\ 1 \\ 1 \\ \vdots \\ 1 \\ 1 \end{pmatrix} \quad \text{and} \quad \vec{b}_N = \begin{pmatrix} 1 \\ b_{N,1} \\ b_{N,2} \\ \vdots \\ b_{N,N-1} \\ -1 \end{pmatrix}. \quad (9)$$

The vector \vec{b}_N does not have a simple form for finite N but the coefficients $b_{N,k}$ go to zero for large N and $k = 1, 2, \dots, N-1$. Notice that this choice of vectors agrees with $\vec{b}_i^T \cdot \vec{a}_j = \delta_{ij}$ in this sub-space. Using these vectors, equation (4) can be re-written, for $k_0 \neq 0, N$, as

$$P(k, t; k_0, 0) = \frac{1}{2}\delta_{k,0} + \frac{1}{2}\delta_{k,N} + \sum_{r=1}^{N-1} b_{rk_0} a_{rk} \lambda_r^t \quad (10)$$

making explicit that extinction is the only asymptotic possibility, independent of the initial state k_0 .

The other eigenvalues and eigenvectors can be calculated from the non-trivial $(N-1) \times (N-1)$ part of U , delimited by the lines in equation (7),

$$V = \frac{1}{2} + \frac{1}{2N}W \quad (11)$$

where

$$W = \begin{pmatrix} 0 & 2 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ N-1 & 0 & 3 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & N-2 & 0 & 4 & \dots & 0 & 0 & 0 & 0 \\ \vdots & \dots & \dots & \vdots & \dots & \vdots & \vdots & \vdots & \vdots \\ 0 & \dots & \dots & \dots & \dots & 4 & 0 & N-2 & 0 \\ 0 & \dots & \dots & \dots & \dots & 0 & 3 & 0 & N-1 \\ 0 & \dots & \dots & \dots & \dots & 0 & 0 & 2 & 0 \end{pmatrix}. \quad (12)$$

If λ_i are the eigenvalues of U , and μ_i the eigenvalues of W , then

$$\lambda_i = \frac{1}{2} \left(1 + \frac{\mu_i}{N} \right). \quad (13)$$

IV. EIGENVALUES AND EIGENVECTORS FOR LARGE N

Although W has a very simple structure, its eigenvalues cannot be calculated analytically for arbitrary N . It can be checked that the resulting polynomial for the eigenvalues μ gets more and more complicated as N increases. However, in the limit $N \rightarrow \infty$, we find

$$\mu_i = N - 2(i - 1) \quad i = 1, 2, \dots \quad (14)$$

The largest eigenvalue, $\mu_1 = N$, yields a new asymptotically stable state, with $\lambda_1 = 1$ and eigenvector

$$a_{1k} = c_1 \exp \left[-2N \left(\frac{k}{N} - \frac{1}{2} \right)^2 \right], \quad (15)$$

corresponding to a symmetric distribution of males and females centered at $k = N/2$. In the limit of large N we may set $\epsilon = 1/N$, $x_k = k\epsilon$ and obtain

$$a(x) = \sqrt{\frac{2}{\pi\epsilon}} \exp \left[-\frac{2}{\epsilon} \left(x - \frac{1}{2} \right)^2 \right], \quad (16)$$

which is the stationary solution of equation (6). For finite N , however, $\lambda_1 < 1$ and the population inevitably goes extinct towards $k = 0$ or $k = N$. Therefore, it is important to estimate how λ_1 tends to 1 as N goes to infinity, a calculation presented in the next section. This provides an estimate of the time to extinction due to fluctuations in the sex determination.

All other values of μ_i lead to $\lambda_i < \lambda_1$ and do not contribute to the asymptotic state of the population. The eigenvectors are given by

$$a_{ik} = c_i \exp \left[-2N \left(\frac{k}{N} - \frac{1}{2} \right)^2 \right] H_{i-1}(\sqrt{2N}(k/N - 1/2)), \quad (17)$$

where $H_m(x)$ are the Hermite polynomials and c_i are normalization constants. The appearance of Hermite polynomials in the solution can be traced to the diffusion equation (6) and its interpretation via Smoluchowski's Brownian motion. These results are demonstrated in the appendix A.

V. LARGEST EIGENVALUE OF W FOR FINITE N

Writing $\mu_1 = N - \alpha$, the eigenvalue equation $\det[W - \mu_1 \mathbf{1}] = 0$ becomes

$$\det[C + \alpha \mathbf{1}] = \det[C] \det[\mathbf{1} + \alpha C^{-1}] = 0, \quad (18)$$

where $C = W - N\mathbf{1}$. Using

$$\det [1 + C^{-1}\alpha] = 1 + \alpha \text{Tr}[C^{-1}] + \mathcal{O}(\alpha^2) \quad (19)$$

we obtain $\alpha = -\{\text{Tr}[C^{-1}]\}^{-1}$,

$$\mu_1 = N + \{\text{Tr}[C^{-1}]\}^{-1} \quad (20)$$

and

$$\lambda_1 = 1 + \frac{1}{2N} \{\text{Tr}[C^{-1}]\}^{-1}. \quad (21)$$

We show in Appendix B that

$$\text{Tr}[C^{-1}] = \sum_{k=1}^{N-1} \frac{f_{k-1}f_{N-k-1}}{f_{N-1}} \quad (22)$$

where

$$f_k = -Nf_{k-1} - k(N-k+1)f_{k-2} \quad (23)$$

with $f_0 = 1$ and $f_1 = -N$. It turns out that, for large N ,

$$\frac{f_{k-1}f_{N-k-1}}{f_{N-1}} = -\frac{1}{N}B(N, k)[1 + \mathcal{O}(1/N)] \quad (24)$$

where $B(N, k)$ is the binomial coefficient. In this approximation the sum can be easily performed and the result is

$$\lambda_1 = 1 - 2^{-(N+1)} \approx 1 - 2^{-N}, \quad (25)$$

which is very accurate even for small N . Setting $\lambda_1 = e^{-1/\tau_e}$ we obtain the time to extinction as 2^N time steps. In terms of number of generations

$$\tau_e = 2^N/N. \quad (26)$$

The last approximation in Eq. (25), where we multiply by a factor 2, is justified because Eq.(24) is accurate only up to the scaling behavior of order $1/N$. The factor 2 is obtained by fitting the numerical simulations (see figure 1). The time to extinction can be related to Ehrenfest model. In this problem N balls are placed in two boxes and a random ball is moved from its box to the other at each time step. Starting from an arbitrary state, the time it takes for finding all the balls in one box is of order 2^N [28]. This is also the Poincaré

recurrence time, which is the time it takes to return to the state with all balls in the same box, having started there.

Considering the meta-stable probability distribution $P(k) = 2^{-N} B(N, K)$ corresponding to λ_1 , one could ask how long it takes for an arbitrary initial state to reach $P(k)$. This is given by the next eigenvalue, $\lambda_2 = 1 - 1/N$, with the associated relaxation time of a single generation:

$$\tau_r = 1. \quad (27)$$

This is the second important time scale of the problem, much shorter than τ_e . This result is analogous to that obtained in [29] for the time taken by a particle to reach the stationary distribution on the hypercube under a nearest neighbor random walk, which is of order $N \log N$.

As a simple example of these time scales, a population with $N = 20$ individuals starting with $k = 10$ females fluctuates according to the binomial distribution after 1 generation, or 20 time steps, but goes extinct only after about $\tau_e = 2^{20}/20 \approx$ fifty thousand generations (or a million time steps). Figure 1 shows a comparison between numerical calculations and the theoretical prediction of τ_e , showing good agreement even for small values of N .

VI. ROBUSTNESS AGAINST CHANGES IN OFFSPRING SEX RATIO

In some species the birth of one of the sexes is favored over the other. A well studied example is the infection caused by the bacteria *Wolbachia*, that kills males in some arthropod species [30]. Sex determination can also be influenced by temperature in several species of reptiles, like the snow skink lizard [31]. Changes in the sex ratio of offspring not only shifts the distribution of males and females in the population but also affects the time to extinction due to random fluctuations. In this section we discuss the time to extinction assuming that the probability of a female offspring is $p = 1/2 + s$ and that of a male is $1 - p = 1/2 - s$.

As we demonstrate below, the inclusion of bias in the sex ratio at birth complicates the dynamics and only approximate solutions for the time to extinction can be derived. However, the problem can be easily solved for the Wright-Fisher model, where generations are non-overlapping and constructed from the previous one by independent random choice of males and females. The Wright-Fisher model describes, for instance, annual plants, where the entire population dies in the winter and its replaced anew in the spring. The Moran

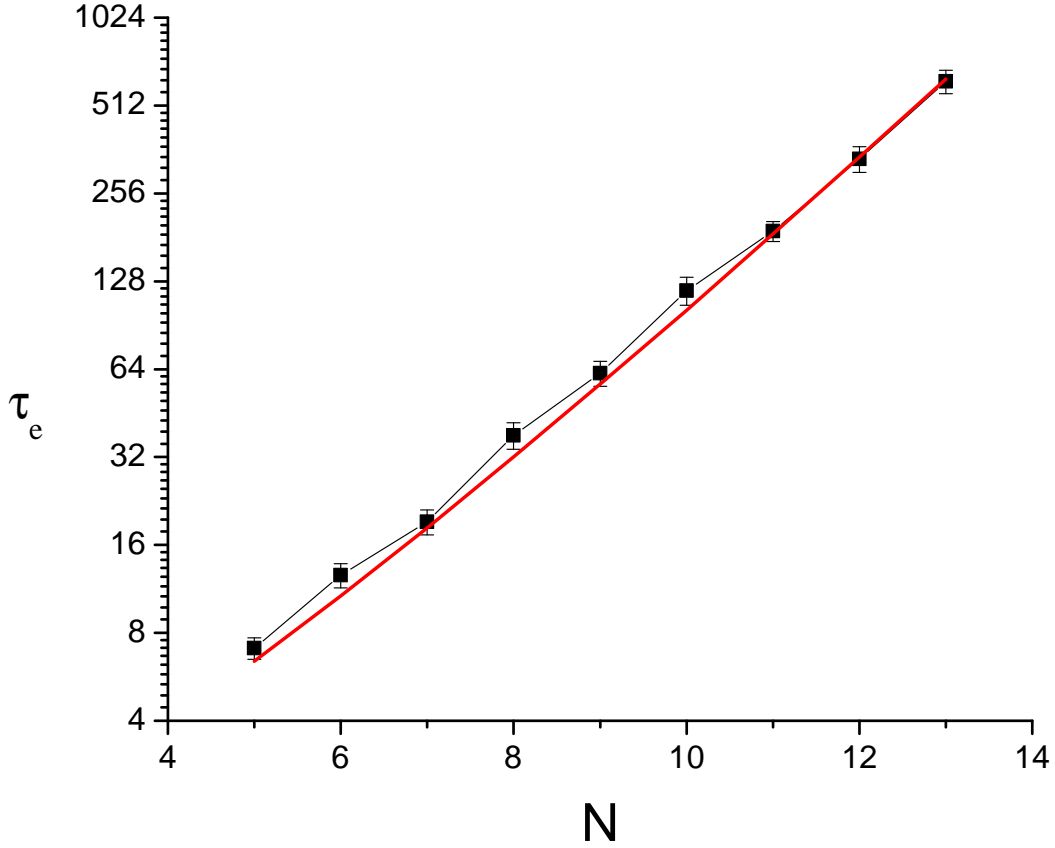


FIG. 1. (Color online) Time to extinction as a function of N . The black points show the average and mean square deviation obtained with 100 replicates of simulations. The red line shows the theoretical result, Eq. (26).

model, on the other hand, is appropriate for perennial plants. The probability of k females is given by

$$(1/2 + s)^k (1/2 - s)^{N-k} B(N, k) \quad (28)$$

and the probability of extinction is, therefore $(1/2 + s)^N + (1/2 - s)^N$, which reduces to $2^{-(N-1)}$ for $s = 0$. The time to extinction is the inverse of this probability and is already given in terms of number of generations: $2^{(N-1)} = (2^N/N) \times (N/2)$. Although this can be taken as a first estimate for the time to extinction in the Moran model, it overestimates it by a factor $(N/2)$ (see Eq.(26)). The factor N comes from updating the entire population at once. Numerical simulations indicate that the factor $1/2$, valid for $s=0$ only, becomes

smaller for more extremes values of s .

In the case of the Moral model, the transition matrix elements are generalized to

$$\Omega_{k,k-1} = \frac{k}{2N}(1 - 2s)$$

$$\Omega_{k,k} = \frac{k}{2N}(1 + 2s) + \frac{N-k}{2N}(1 - 2s) = \frac{1}{2N}(N + 2s(2k - N)) \quad (29)$$

$$\Omega_{k,k+1} = \frac{N-k}{2N}(1 + 2s)$$

and a master equation similar to equation (1) can be written. In the extreme cases $s = \pm 1/2$ all the eigenvalues of the evolution matrix U can be calculated analytically and the largest non-unit eigenvalue is $\lambda_1 = 1 - 1/N$, so that the time to extinction is approximately N , i.e., 1 generation.

In the limit of large N , the master equation can also be written as a diffusion equation

$$\frac{\partial P}{\partial t} = \frac{\partial}{\partial x} \left[D(x, s) \frac{\partial P}{\partial x} \right] - \frac{\epsilon}{\delta} \frac{\partial}{\partial x} [F(x, s)P] \quad (30)$$

with a 'space-dependent' diffusion coefficient $D(x, s) = (\epsilon^2/4\delta)(1 + 2s - 4sx)$ and $F(x, s) = -(x - 1/2 - s - \epsilon s)$. The stationary solution is

$$P(x) = A \exp \left\{ \frac{4sx + [1 - 4(1 + \epsilon)s^2] \ln(1 + 2s - 4sx)}{4\epsilon s^2} \right\}, \quad (31)$$

where A is a normalization constant. Notice the symmetry of these equations with respect to the change $s \rightarrow -s$ and $x \rightarrow 1 - x$.

Differential equations for the continuous limit of the coefficients a_k and b_k can also be obtained and the corresponding solutions are $\mu_i = N - 2(i - 1)$ with

$$b_i(x) = c_i H_{i-1} \left(\sqrt{\frac{2N}{1 - 4s^2}} (x - 1/2 - s) \right) \quad (32)$$

and

$$a_i(x) = d_i \exp \left\{ -\frac{2N(x - 1/2 - s)^2}{1 - 4s^2} \right\} b_i(x), \quad (33)$$

where $H_i(x)$ are the Hermite polynomials. Although the solution for $a_1(x)$ looks rather different from (31), they are very similar for large N . Equation (33) for $i = 1$, corresponding to $\mu_1 = N$, is just a Gaussian centered at $x = 1/2 + s$ with variance $1 - 4s^2$, as it should be.

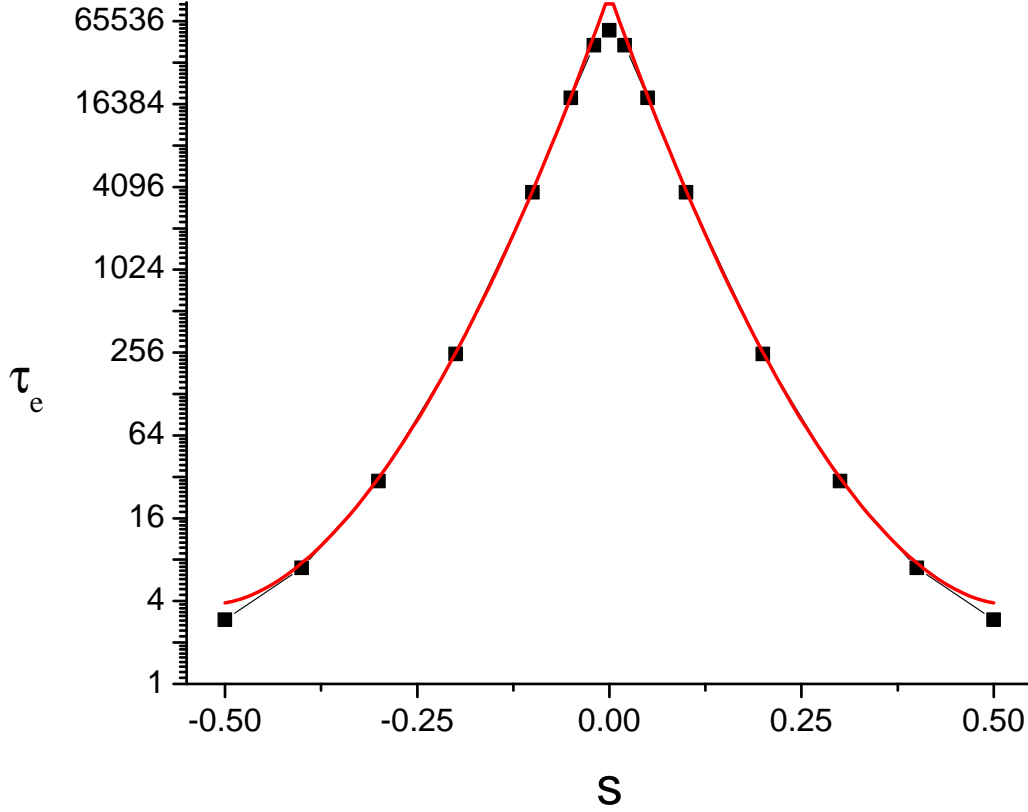


FIG. 2. (Color online) Time to extinction as a function of s for a population with $N = 20$ starting with 10 males and 10 females. The line with square symbols shows the result of simulations obtained from 10,000 realizations for each value of s . The thick red line shows the approximation $\tau_2 = a2^{N_{eff}}/N_{eff}$ for $a = 2$.

The correction to the μ_1 is still given by equation (20) but now with

$$Tr[C^{-1}] = \sum_{k=1}^{N-1} \frac{f_{k-1}(-s)f_{N-k-1}(s)}{f_{N-1}(s)} \equiv \sum_{k=1}^{N-1} d(N, k, s) \quad (34)$$

where

$$f_k(s) = -[N + 2s(N - 2k)]f_{k-1}(s) - k(N - k + 1)(1 - 4s^2)f_{k-2}(s) \quad (35)$$

with $f_0 = 1$ and $f_1 = -N + 2s(N - 2)$. Explicit evaluation of the coefficients $d(N, k, s)$, however, is much more complicated and an analytic expression is not available. Numerical

simulations show that, for large N , we may approximate

$$d(N, k, s) = -\frac{A(N, s)}{N} \exp \left\{ -\frac{2N(k/N - 1/2 - s)^2}{1 - 4s^2} \right\} \quad (36)$$

where

$$A(N, s) = 2^{N(1-1.4|s|)^2} \quad (37)$$

was obtained by fitting the amplitude of the coefficients. Further approximating the sum over k in equation (34) by an integral we obtain

$$Tr[C^{-1}] = -A(N, s) \sqrt{\frac{\pi(1 - 4s^2)}{2N}} \quad (38)$$

so that the time to extinction becomes

$$\tau_e = 2 \sqrt{\frac{\pi(1 - 4s^2)}{2N}} 2^{N(1-1.4|s|)^2} \sim 2^{N_{eff}} \quad (39)$$

with $N_{eff} = N(1 - 1.4|s|)^2$. Figure 2 shows the time to extinction as a function of s for $N = 20$. The solid line shows the result of simulations and the red line a fit with $\tau_2 = a2^{N_{eff}}/N_{eff}$. The goodness of the fit suggests that the expression is correct and that the main effect of s is to change the population size to an effective value.

Our calculations have shown that producing males and females offspring at the same proportion is a good strategy even for very small populations. If, however, the birth of one of the sexes is favored, not only the balance between males and females is altered but the time to extinction might decrease dramatically. For small deviations, however, the exponential character of the extinction time remains.

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Appendix A: Eigenvalues and eigenvectors of W for large N

Setting $a_{i0} = a_{iN} = b_{i0} = b_{iN} = 0$ we obtain the following recurrence relations for the i -th right and left eigenvectors of W :

$$(k + 1)a_{ik+1} + (N - k + 1)a_{ik-1} - \mu_i a_{ik} = 0 \quad (A1)$$

and

$$(N - k)b_{ik+1} + kb_{ik-1} - \mu_i b_{ik} = 0. \quad (\text{A2})$$

It can be checked that these components are related by

$$a_{ik} = 2^{-N} Bi(N, k) b_{ik}, \quad (\text{A3})$$

where $Bi(N, K)$ is the binomial coefficient.

Dividing equation (A2) by N and defining the function $\tilde{b}_i(x)$ such that $\tilde{b}_i(x_k) = b_{ik}$ leads to

$$(1 - x)\tilde{b}_i(x + \epsilon) + x\tilde{b}_i(x - \epsilon) - \frac{\mu_i}{N}\tilde{b}_i(x) = 0, \quad (\text{A4})$$

where $\epsilon = 1/N$.

For $N \gg 1$, we can approximate $\tilde{b}_i(x \pm \epsilon) = \tilde{b}_i(x) \pm \epsilon \tilde{b}'_i(x) + \frac{\epsilon^2}{2} \tilde{b}''_i(x)$. Neglecting terms of $O(\epsilon^3)$, equation (A4) is turned into a differential equations for $b(x)$:

$$\tilde{b}''_i \frac{\epsilon^2}{2} + \tilde{b}'_i \epsilon (1 - 2x) + \tilde{b}_i \left(1 - \frac{\mu_i}{N}\right) = 0. \quad (\text{A5})$$

Taking the limit $N \rightarrow \infty$ ($\epsilon \rightarrow 0$) we see that $\mu_1 = N$ is an eigenvalue. The corresponding left and right eigenvectors are given by

$$b_{1k} = 1, \quad a_{1k} = 2^{-N} \frac{N!}{k!(N-k)!} \text{ for } k = 1 \cdots N - 1. \quad (\text{A6})$$

To obtain the remaining eigenvalues and eigenvectors for large N we define $t \equiv \sqrt{2N}(x - 1/2)$ and the function $g(t) \equiv \tilde{b}(\frac{t+1/2}{\sqrt{2N}})$. Accordingly, equation (A5) becomes

$$g''_i - 2tg'_i + 2d_i g_i = 0 \quad (\text{A7})$$

where $d_i \equiv (N - \mu_i)/2$. Equation (A7) is satisfied by the Hermite polynomials if d_i were integers. To see that this is indeed the case, note that the boundary conditions are $\tilde{b}(0) = \tilde{b}(1) = 0$, where the argument is $x = t/\sqrt{2N} + 1/2$. Therefore, the corresponding boundary conditions for $g(t)$ are $g(\pm\sqrt{N/2}) = 0$ or, for $N \rightarrow \infty$, $g(\pm\infty) = 0$. In order to prevent $g(t)$ from diverging we must set $d_i = 0, 1, 2, \dots$. The procedure is similar to the quantization of the harmonic oscillator in quantum mechanics. In this limit the eigenvalues and eigenfunctions are given by

$$\mu_i = N - 2(i - 1) \quad (\text{A8})$$

and

$$g_i(t) = c_i H_{i-1}(t) \quad (\text{A9})$$

or

$$b_{ik} = c_i H_{i-1}(\sqrt{2N}(k/N - 1/2)) \quad (\text{A10})$$

where $i = 1, 2, 3, \dots$ and the c_i are normalization constants.

For the right-eigenvectors we can approximate the binomial by the normal distribution $Bi(p, N) \approx N(\mu, \sigma)$ by taking $p = 1/2$, $\mu = Np$ and $\sigma = Np(1 - p)$. We obtain

$$a_{ik} = c'_i \exp[2N(k/N - 1/2)^2] H_{i-1}(\sqrt{2N}(k/N - 1/2)). \quad (\text{A11})$$

Appendix B: The trace of C^{-1}

The matrix C is given by

$$C = \begin{pmatrix} -N & 2 & 0 & 0 & \dots & 0 & 0 & 0 & 0 \\ N-1 & -N & 3 & 0 & \dots & 0 & 0 & 0 & 0 \\ 0 & N-2 & -N & 4 & \dots & 0 & 0 & 0 & 0 \\ \vdots & \dots & \dots & \vdots & \dots & \vdots & \vdots & \vdots & \vdots \\ 0 & \dots & \dots & \dots & \dots & 4 & -N & N-2 & 0 \\ 0 & \dots & \dots & \dots & \dots & 0 & 3 & -N & N-1 \\ 0 & \dots & \dots & \dots & \dots & 0 & 0 & 2 & -N \end{pmatrix}. \quad (\text{B1})$$

and we only need the diagonal elements of C^{-1} , which can be obtained by Laplace's formula:

$$[C^{-1}]_{kk} = \frac{\text{Cofactor}(k, k)}{\text{Det}[C]}. \quad (\text{B2})$$

The Cofactor(i,j) is the determinant of the auxiliary matrix obtained by removing the j-th line and i-th row of C , multiplied by $(-1)^{i+j}$.

The removal of the k-th line and row of C divides the remaining matrix into two decoupled blocks. In order to deal with these blocks we recursively define the matrix C_{N-k} to be the matrix C_{N-k+1} with the first line and first row removed. This definition holds for $k = 2, \dots, N-1$, with the initial condition $C_{N-1} \equiv C$. Calling $f_{N-k} = \text{Det}[C_{N-k}]$ it is easy to see that

$$\text{Cofactor}(k, k) = f_{k-1} f_{N-k-1}. \quad (\text{B3})$$

Applying the Laplace rule to the determinant f_k it can be checked that it satisfies the recurrence relation

$$f_k = -Nf_{k-1} - k(N - k + 1)f_{k-2} \quad (\text{B4})$$

with $f_0 \equiv 1$ and $f_1 \equiv -N$.

In order to calculate (B3) it is useful to define $g_k = (-1)^{k+1}f_{k-1}/k!$. In terms of g_k the recurrence relation becomes

$$(k+1)g_{k+1} - Ng_k + (N - k + 1)g_{k-1} = 0 \quad (\text{B5})$$

with $g_0 \equiv 0$ and $g_1 \equiv 1$. We obtain

$$[C^{-1}]_{kk} = \frac{f_{k-1}f_{N-k-1}}{f_{N-1}} = -\frac{g_k}{g_N} \frac{1}{B(N, k)} \quad (\text{B6})$$

where $B(N, k)$ is the binomial coefficient. Since (B5) is the relation satisfied by $B(N, k)$ itself, it is reasonable to assume that

$$g_k = \frac{1}{N}B(N, k) \quad (\text{B7})$$

where the factor $1/N$ guarantees the initial condition $g_1 = 1$. This, however, is only an approximation, since it gives $g_0 = 1/N$ and not zero. However, for large N it suffices for obtaining the first order correction to the eigenvalue. Replacing (B7) into (B6) we obtain

$$[C^{-1}]_{kk} = -\frac{B(N, k)}{N}. \quad (\text{B8})$$

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